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FOCAL ARTICLE

COMPARATIVE PSYCHOLOGY AND THE RECURSIVE STRUCTURE OF FILTER EXPLANATIONS

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ABSTRACT: Over the last three decades many critics have worried that the theory of adaptation by natural selection is a circular explanation and has no empirical content. We argue, however, that the theory is not circular but recursive. In a recursive explanation the explanandum serves to specify which of a class of potential explainers is being appealed to. Many explanations thought to be circular are in fact recursive, including the classical exemplar of a circular explanation, Moliere's *virtuus dormitiva*. Natural selection theory is a recursive explanation in which the thing to be explained serves to specify a particular Darwinian filter. Unlike circular explanations, recursive explanations can have considerable explanatory value. That value depends somewhat independently on the two parts of a recursive explanation, its explanatory frame and its recursion. The frame of a Darwinian explanation is valuable because it tells us that the trait in question is a result of a Darwinian filter. For instance, to say that the polar bear's fur is white because of natural selection is informative. It says that in the past there were bears of various colors and that over the generations only white bears have passed through the filter until now all bears are white. The value of the recursion of a Darwinian explanation depends on the characterization of the explanandum that occurs in the recursion. An overspecified explanandum leads to an ad hoc Darwinian explanation. An underspecified explanandum leads to a vague Darwinian explanation. While both of these are strictly speaking explanatory, they lack the heuristic value that would earn them the respect of working scientists. To have heuristic value, a Darwinian filter explanation requires characterization of the explanandum in terms of intermediate generality. This analysis suggests that the future of Darwinian theory depends on revival of systematic comparative description.

Comparative Psychology may be thought of as the discipline where two bodies of theory potentially interact: learning theory and Darwinian theory of evolution. Many commentators have observed that these two theories have the same general structure (Nozick, 1974, pp. 18-22, 312-317; Bateson, 1979; Thompson, 1981). Both are filter theories. In

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both, a current feature of the behavior or structure of organisms is explained by claiming that this feature has been filtered from a range of features produced by the organisms at an earlier time.

Since the two theories have a similar structure, it would also be expected that they would have similar logical problems. One such problem shared by the two theories is that both are frequently attacked for their alleged circularity. The charge that an explanation is circular must be taken seriously because circular explanations do not in fact explain. They merely restate the question they claim to answer. They are particularly pernicious in science because they give a false sense of understanding and prematurely put a stop to scientific inquiry. Because learning theory and evolutionary theory are so central to comparative psychology, the discovery that both are logically circular would be a devastating discovery for theoretical development in the field.

In this essay, we examine the alleged circularity of one of the two theories, Darwin's theory of evolution by natural selection. Our general conclusion is that while Darwinian explanations are rarely circular even in the most careless hands, they do have a peculiar logical structure that makes them both easy to confuse with circular explanations and vulnerable to other explanatory hazards. We will not treat learning theory in detail. However, because learning theory is also an example of a filter explanation, our comments about the logical vulnerability of Darwinian theory will have relevance to learning theory as well.

INTRODUCTION

In the central theorem of Darwinism an explanandum state, adaptation, is explained by an explanans process, natural selection. The terms, 'explanandum' (= the thing one is trying to explain) and 'explanans' (= the thing that is doing the explaining) are standard philosophical terminology. Because one of the authors (N.S.T.) is forever confusing them, we will back up our usage of these terms with the equivalent expressions, wherever we can do so without making the text impossibly wordy.

Adaptation, the thing that requires explanation, is the suitability of organisms to their circumstances. Organisms, unlike most of the other natural objects of our world, have the property of being more or less well-designed for the worlds in which they live. In the context of a scientific materialism that denies the possibility of intentional creation, this semblance of designedness in organisms is anomalous.

Natural selection, the thing that explains the anomaly, is the differential reproduction of organisms bearing one type of heritable trait by comparison with those that bear its alternative. Natural selection theory reconciles the apparent designedness of organisms with scientific mate-

rialism by making an analogy to the manner in which elaborate breeds of pigeons are produced by pigeon fanciers. Just as the circumstances of the pigeon coop assure that those pigeons with the elegant feathers, flight patterns or courtship routines have the most offspring, so the circumstances of nature assure that in general those organisms which are better adapted to their circumstances will have more offspring than those less well adapted. And if such a reproductive bias continues, either in the pigeon coop or in nature, then it assures in time that pigeons will have elegant feathers, or flight patterns or courtship routines and that organisms in nature will be better designed for their circumstances. Thus adaptation exists for the same reasons that elegance in pigeons exists: because it corresponds to an aesthetic bias in the life environment of the organism (Rindos, 1984).

The putative circularity arises in the following way. The two concepts linked by Darwinian theory, natural selection and adaptation, have very different strengths and weaknesses. While there is a wide agreement that organisms possess the property of adaptation, there is no widely accepted way to define that property. It is, in fact, an exceedingly complex property. To say that an organism is well-designed for a set of circumstances, is to say that being like this organism facilitates the solution of some characteristic "problem" posed by these sorts of circumstances (Dunbar, 1982). Revealing this property of organisms is the province of comparative anatomy and bioengineering (Thompson, 1981; Lewontin, 1978; Williams, 1966; Sommerhoff, 1950). We can grasp it intuitively because it is very like the manner by which we judge the functions of ordinary objects and the intentions of people and animals. Because we can grasp adaptation intuitively, we can easily point to good examples of it in nature.

But to say that something can be intuitively grasped and readily pointed to is a long way from saying that it is sufficiently well-defined for scientific purposes. While intuition is sufficient to lead us to the good examples of a phenomenon, it is rarely sufficient to sort out the borderline cases in a manner consistent with modern scientific practice. Scientific concepts must be reliable and explicit in their application, and unelaborated intuitive criteria cannot pass this test. Moreover, adaptation as it is currently understood is a mathematically intractable concept. No measures have been agreed upon by which we can say how well or how poorly adapted an organism is to particular circumstances. Consequently, of adaptation, we can say that it is readily exemplified, but poorly defined and mathematically intractable.

Natural selection has many of the complementary virtues and vices. Unequivocal instances of natural selection are difficult to point to. It is rarely shown that a particular well-designed property of an organism has come about through a history of differential reproduction of better designed variants (Hailman, 1982). But natural selection is readily

defined and its mathematics has been thoroughly developed. Consequently, of natural selection we can say that it is difficult to exemplify, but that it is well-defined and possesses a tractable and powerful mathematics.

Under these circumstances it is understandable why modern science, with its fondness for precise definition and mathematical modeling should be tempted to define adaptation in terms of natural selection. Such a redefinition occurs when the better-adapted organism is defined as the one that has more than its share of offspring. Surprising as it may seem, adaptation is frequently redefined in this way in the literature. In fact, the redefinition is deeply entrenched in classical literature of population biology, for which the central term, "fitness" refers not to some property of appropriateness or suitability to the environment but simply to the relative number of offspring of an organism.

The redefinition has the advantage that it supplies each of the key evolutionary concepts, natural selection and adaptation, with something it lacks. To natural selection it supplies a method of pointing to cases of natural selection at work: each of the obvious cases of adaptation in nature becomes an unequivocal case of a product of natural selection. To adaptation, it supplies a clear definition and access to a sophisticated mathematics: each unequivocal case of adaptation can be precisely defined and analyzed using natural selection mathematics.

The redefinition has the disadvantage that it opens evolutionary theory to accusations of circularity. If the adapted animal is defined as the one that produces the most offspring, then the claim that all animals that are adapted are favorably selected is analytically true and beyond empirical validation. To search for cases to validate the statement that all animals that are selected are adapted under these circumstances would be like conducting a door-to-door survey of bachelors to discover if they are unmarried. The hypothesis will always be validated.

Over the last two decades, a vigorous argument has been conducted over whether this allegation of circularity is well founded, whether the alleged circularity is pernicious and whether, if pernicious, it is avoidable. Some have argued that it is not pernicious. Karl Popper once (1972, as cited—and recanted!—in Popper, 1978) argued, for instance, that the circulatory is not pernicious because Darwinian theory is not an explanation but a "metaphysical research programme" (p. 344) which should be evaluated not for its truth or falsity but for its capacity to help the scientist generate propositions whose truth can be tested. This response, while safe enough, seems monstrously to underestimate the accomplishments of Darwin. The fact is that Darwin's theory constituted an alternative and better explanation of adaptation than the theories of its day. To relegate the modern version of that theory to a heuristic world view is to set the growth of knowledge back a century.

Some have argued that the putative circularity is the result of a confusion between what adaptation actually is and how it can be known. Rosenberg (1980b), for instance, makes a very persuasive argument for the logical distinctness of adaptation and natural selection. But he insists that adaptation is beyond any reasonable possibility of direct scientific treatment and that we must therefore use differential reproduction as the "only practicable general means" of assessing the degree of adaptation of an organism. This argument seems like the scientific equivalent of using the reticence of the suspect as a rationale for torture. It suggests that the greater our practical need to reason circularly, the greater is our justification in doing so.

Some have argued that the circularity is pernicious, but avoidable. Thompson (1981), for instance, points out that the comparative method, a widely respected descriptive method in biology, could form the basis for the specification of adaptation necessary to evolutionary theory and that biologists should work harder at elaborating and formalizing the comparative method as a means of defining and quantifying adaptation (see also Lewontin, 1978).

We now believe that all of these earlier accounts are either incorrect or irrelevant because natural selection explanations are not strictly speaking circular, neither essentially nor as they are practiced. They are, in fact, recursive. The difference is crucial because while circularity in an explanation is a terminal disease, recursion can be healthy and it may even constitute an important preliminary stage in Darwinian explanation. On the other hand, despite the virtues of recursive explanations, they do have their own peculiar vulnerabilities. A theorist who would make use of recursive explanations must understand their limitations or run the risk of making statements that are almost as empty and fatuous as a circular explanations.

THE STRUCTURE OF RECURSIVE EXPLANATIONS

One of the best ways to understand the structure of a recursive explanation is to see how it differs from that of a circular one. In a circular explanation, the explanans is a restatement of the explanandum. For instance, if we answer the question, why are polar bears white? with the reply, "Because they are white!" we have given a circular explanation. Even the reply, "because of their alabaster hue!" would be circular because it is just a dressy way of saying "white." Thus, the explaining concept is simply a restatement of the thing it explains.

In a recursive explanation, the explanans contains a restatement of the explanandum embedded in a larger structure. If the question is, "what makes polar bears white?" then the answer, "Because there is a

force in the environment that makes them white!" is recursive, not circular. Even though "makes them white" is a paraphrase of the question, the introduction of the words "force in the environment" embraces the paraphrase in a nonparaphrasing explanation and breaks the logical circle. This recursive explanation does not treat the color of the fur as literally self-explanatory, as does a circulatory explanation; instead it uses the color as a way of specifying something else as the explanation, in this case, the force that brought it about.

Since a recursive explanation does use the explanandum in the explanans, recursive explanations are easily confused with circular ones. Distinguishing them requires a careful comparison of the explanandum with the explanans, that is, of the question with the answer. If the question above had been, "which is the force which makes polar bears white?", then the answer, "The white-making force!" would be circular because that answer is a restatement of that question. In general terms, if a question is of the form, "why is E?", then an explanation is circular if it is of the form, "because of E!", but merely recursive if it is of the form "Because of the cause of E!". A recursive explanation is more informative than a circular explanation just to the extent that we have independent sources of information about the class of causes referred to in the explanation.

What does it mean to say that an explanation is more informative? One way of measuring the information value of an explanation is by the "exclusion test." Better explanations, according to this view, are explanations that exclude more possible causes. Let's imagine that we are trying to explain the "snow" on the screen of our computer. Two explanations are offered us: one, that the snow is caused by a "malfunction in the computer" and two, that the snow is caused by a "glitch in the monitor." Both explanations exclude many causes, for instance, problems in radio interference from outside the computer. Of the two, the second explanation is better because it excludes all the alternative causes that the first explanation excludes and more. For instance, if the "glitch in the monitor" account is correct, we know that we need not look in the central processing unit for the source of our problem.

Circular explanations fail the exclusion test. They are uninformative in that they exclude no alternatives. The claim that the bear is white because it is white is compatible with every possible cause of the bear's fur color. Recursive explanations, by contrast, usually do exclude some alternatives and, by the exclusion test, vary in quality from those that exclude very few alternatives to those that exclude many.

The weakest recursive explanation is one of the form, "X because of the cause of X." This explanation excludes no causes. At most it excludes the possibility that X was uncaused. Nearly as weak is the explanation deployed by Moliere's Doctor in *Le Malade Imaginaire* to explain the

sleep-inducing effects of opium. "Why," the Doctor is asked, "Does opium put people to sleep?" "Because," he replies, "it possesses a *virtuus dormativa* (a sleep-inducing power)." Often represented as the archetypal circular explanation, the Doctor's response is not circular but a weak recursive explanation. Even though the *virtuus dormativa* is very nearly a restatement of the question, the *virtuus dormativa* is not the whole explanation. The whole explanation includes the words "it possesses" and this frame gives us some little hint about where to look or where not to look for opium's sleep-inducing effects. For instance, the effects do not have their source in the social environment associated with the drug. They are not hypnotic effects. Nor do they come from the act of smoking, per se. They are not, for instance, the result of carbon monoxide the smoker inhales on account of the incomplete combustion in the opium pipe. But much as it excludes, the explanation is a fairly weak one because we are told nothing of the sleep-making mechanism, only that it is located in the drug.

Intention explanations are also weak recursive explanations. When we answer the question "Why did he do X?" with "Because he intended to do X!", the intention frames the paraphrase of the question. While not therefore strictly speaking circular, intention explanations suffer from difficulties both with their frames and with their recursions. The framing relation, intention, is notoriously difficult to specify (Rosenberg, 1980a).

Thus far we have been providing examples of recursive explanations that are relatively weak. Not all recursive explanations are as weak as intention explanations or *virtuus dormativa* explanations. Filter explanations can be quite informative, even though recursive. Consider the explanation, "The oil is clean because it has passed through a clean oil filter." Such a filter explanation answers a question of the form, "why are all the X's Y?" with the reply, "Because they have passed through a Y-filter!" A filter explanation accounts for the characteristics of an aggregate as a result of a process in which every individual in an earlier aggregate was examined for its possession or nonpossession of some criterional attribute; those possessing the attribute were permitted to pass, those not possessing it were not, so that every individual in the post-filter aggregate meets the criterion of the filter. Filter explanations are informative because, no matter how ignorant we may be about the criterion, the explanation tells us that:

- (1) Somewhere, sometime, there was an initial aggregate of X's which were both Y and not Y.
- (2) There is a process which distinguishes X's that are Y from X's which are not Y and selects the former.
- (3) The present aggregate is the result of the application of the process in (2) to the initial aggregate in (1).

This information excludes at least three possibilities: that the present aggregate is a chance occurrence, or that there never were anything but Y individuals or that all the not-Y individuals mutated into Y's.

Because filter explanations are relatively informative, they have a respectability as explanations that circular explanations and weaker recursive explanations don't have.

EVALUATING DARWINIAN EXPLANATIONS

Darwinian explanations are filter explanations. They answer questions like, "Why are polar bears white?" The sort of answer they give is, "Because, in the history of the species, those bears that matched their surroundings had more offspring than those that didn't with the result that white fur came to characterize the species!" The explanation attributes to the environment a "white bear filter" which limited access to the successive generations to paler bears until all bears were white. No matter how loose is our grasp of the details of the filter mechanism, we know two things about any Darwinian filter explanations. We know that it is not circular because it is recursive. And we know that it has a relatively high value among recursive explanations because it is a filter explanation.

Everything we have said so far concerning Darwinian filter explanations applies to all members of the class. We are left, therefore, with the question, "How do we tell the difference between good Darwinian explanations and not so good ones? By what standard do we evaluate Darwinian filters?" A standard commonly used to measure theories is their generality. This standard is particularly important to scientists, who are always trying to extend the range of application of their concepts. For such purposes, a theory is valuable just to the extent that it can be generalized to many situations. A theory which explains the snow on our computer screen in terms of a glitch in the monitor is useful for the operator of this computer, but it is too specific to give guidance about how this sort of fault comes about.

A better theory explains the snow by reference to a fault in the machine that etched the circuit board in the monitor. Not only does it explain the same fault in other monitors coming from the same factory, it may also explain different faults in the same computer or even faults in other electronic equipment employing the same etching technique. It is this sort of theory that will be most attractive to engineers interested in computer design. For scientific purposes a theory is most valuable when it offers a principle that will explain large classes of particulars. It is, in this sense, a more general theory.

But generality is not the simple good that exclusivity is. Theories can be too general. The theory that I have snow on the screen of my computer

because computers are prone to snow-formation under some circumstances is a very general theory but it is so vague that it provides little guidance either to me or to a computer engineer. Thus, for scientific purposes, the best theories seem to display a moderate degree of generality: general enough to cover many instances, specific enough to avoid vagueness (Garfinkel, 1981, pp. 30-1; Hull, 1974, p. 68). Just where the "golden mean" for an explanation will lie depends on many factors, including the interests of the investigator.

On first consideration, it might appear that the generality and exclusivity tests conflict with one another, but in fact the two criteria work together. Exclusivity refers to the number of causes an explanation excludes; generality to the number of cases in which the cause is excluded. Over-general explanations are bad because they exclude few causes; over-specific explanations are bad because they exclude causes in very few cases.

Like other explanations, Darwinian filter explanations are better if they have a moderate degree of generality. If the characterization of the filter is too specific, the resulting explanation will be ad hoc and too difficult to integrate with accounts of other filter mechanisms. If, on the other hand, the characterization of the filter is too broad, the only way to specify a unitary mechanism behind it is to make that mechanism so vague as to be uninformative.

With respect to generality, there is one critical difference between ordinary explanations and recursive explanations. In nonrecursive explanations, the generality of the explanation is independent of the generality of the phenomenon which is being explained. The highly specific question concerning why a particular ball fell at a particular time may be answered by appeal to the very general theory, Newton's theory of gravitation. But with Darwinian filter explanations, because of their recursive structure, the generality of the explanatory principle is determined by the generality of the terms by which the thing to be explained is described. In short, the generality of the explanans is determined by the generality of the explanandum, because the latter is incorporated in the former. For example, if the question is asked at the level of the polar bear's white fur, the recursive answer—that there is a white fur filter—it must be made at the same level. Thus, the requirement that explaining principles be moderately general places a special burden on recursive explanations. For recursive explanations, this requirement entails that the thing to be explained must also be characterized at a moderate level of generality because the characterization of the thing to be explained appears in the explanation. Thus, what is in general an obligation of scientists to give the right sort of answer becomes, for Darwinian scientists, the requirement that we ask the right sort of question.

This analysis suggests that if research is to progress in the explanation of behavior through natural selection, then close attention must be paid to the descriptions we give phenomena and the questions we ask of them. On the one hand we must avoid questions that are excessively general, such as, "Why have contemporary organisms survived?" The recursive answer, that they have passed through a survival filter, while not circular, is uninformative because it is compatible with any and all mechanisms of survival and provides no guidance to which different sorts of mechanisms underly the perseveration of different species. At the other extreme are questions which request explanations concerning the behavior and morphology of single species. The simple question concerning polar bear fur which we have been using throughout this essay, while useful for illustrative purposes, is actually an example of an overspecified question. By asking the question "Why are polar bears white?" we are led by the recursive structure of our explanation to posit a white bear filter. This explanation is correct as far as it goes and can be backed by a specification of the mechanism that constitutes a white bear filter, but it requires us to develop an entirely new explanation whenever we encounter another kind of mammal in another kind of environment.

IMPLICATIONS FOR EVOLUTIONISTS

We began this essay with a brief recounting of the ambivalence that philosophers and others have expressed concerning the Darwinian theory of evolution. Is it a good theory abused by its practitioners or an overused trivial truism? Is it a theory at all, or merely a meta-theoretical commitment? We are now in a position not only to answer these questions but to make clear the sources of confusion from which they arise and to make suggestions for how problems may be avoided in the future.

Darwinian theory is not circular. It is an example of a recursive theory, a kind of theory in which the thing to be explained is not identical to the thing which explains, as in a circular explanation, but is included within the thing which explains. Darwinian recursive theories are filter theories and they gain some considerable explanatory value from the notion of a filter, whether or not the criterion of the filter is specified. As a consequence, no Darwinian theory is a truism nor is it just a meta-theoretical commitment. Darwinian theories are real theories.

Given the similarity of recursive and circular explanations, however, it's easy to see how the two might get confused. The traditional method for identifying a circular explanation is to discover the explanandum lurking in the explanans. As we have seen, this criterion, while necessary to circularity, is not sufficient for it. To be circular, an explanation must *only* repeat the explanandum in the explanans, and this error is avoided by recursive explanations. Of course, recursive explanations vary in

quality. Some recursive explanations, notably Darwinian filter explanations, do provide considerable information. But most recursive explanations, such as the *virtuus dormitiva* of Moliere, provide relatively little additional information and are therefore difficult to distinguish from genuinely circular explanations. Thus, if philosophers have failed to notice that not all explanations are circular which include the thing to be explained within them, then practicing scientists may be forgiven for making the same oversight.

Having said that the informativeness of Darwinian filter theory protects us from making genuinely circular explanations, we must quickly add that it does not protect us from making fools of ourselves. Darwinians can be as pretentious as Moliere's Doctor if they fail to make a distinction between appealing to Darwinian filter explanations as a class and appealing to a well-specified Darwinian filter explanation. The distinction is not all that easy to make and may be determined by such subtle factors as the assumptions of the audience to which the Darwinian expert is speaking. Before a convention of creationists, the assertion that Darwinian filters explain the biological world is extremely informative, even though it includes no specification of how the world has turned out and therefore only the vaguest sort of specification of the filter. Similarly, an overly narrow filter explanation, such as claiming that the polar bear is white because it has been selected for its whiteness, might be appropriately delivered over the loudspeaker system of an arctic tour boat, even though it gives little guidance for the characteristics of organisms other than polar bears.

But the same statements would be worthless made before a convention of biologists, comparative psychologists, or ethologists. Such explanations should be treated with contempt by such an expert audience because they add nothing to the assumptions that Darwinian scientists already bring to the occasion. The frequency of such misappropriations of Darwinian logic may arise in part from the enormous traffic that has recently occurred in evolutionary behavioral biology between writing for the lay reader and writing for professionals. Having been rewarded both financially and intellectually for offering unelaborated Darwinian explanations to lay audiences, Darwinians are tempted to try them on their colleagues. This temptation is enhanced by the fact that so fragmented have the biological sciences become that each of us seems a lay person to each of the others. This trend has gone so far that the titles of professional papers seem to market their authors and ideas as baldly as advertisers do their products. The temptation to offer over- or under-specific Darwinian explanations to professional audiences should of course be resisted. In that context, such explanations are foolish at best and at worst a form of scientific demagoguery.

In order to avoid this sort of error, scientists need to be aware of the distinction between two components in the value of an explanation, the

intrinsic and the heuristic components. Intrinsic value is the power of the explanation to answer inquiries; heuristic value is its power to prompt additional inquiries. Even the barest of Darwinian filter explanation has intrinsic explanatory value, if only because it commits the explainer to Darwinian selection as an explanation, rather than, say, to some form of creation theory. But as we have already observed, such intrinsic value is of no use to Darwinians. For Darwinian audiences, Darwinian filter explanations must provide an additional kind of value, a heuristic value. Thus, for questioners seeking a more specific causal account of the phenomenon, recursive explanations serve a directive function. They serve as a transitional step in our understanding of a phenomenon that permits us to talk about an explanation before we have it fully fleshed out with a causal story which connects the circumstances of the organism with the output of the filter.

The power of this heuristic component can be illustrated by an example familiar to all comparative psychologists; the classical research of Tinbergen et al. (1962) on the gulls' habit of removing eggshells from their nests. At a very early stage in his understanding of that behavior, Tinbergen relied heavily on his faith that the behavior existed because it was selected for. The force of this preliminary explanation is that there exists in the environment some sort of "eggshell removal" filter and the effect of making that explanation was to send Tinbergen out into the gulls' environment looking for the factors which might constitute the filter. Through his comparative analysis and experiments, Tinbergen rejected the idea that risk of damage or contamination to the chicks from the eggshells constituted the filter and settled instead on the idea that the filter was the visual discrimination of the nest sites by carrion crows and other visual predators. The bright, uncamouflaged inner surface of the egg helped carrion crows to locate the nests and resulted in nests with broken eggshells losing more chicks to predators than nests without. Thus, when Tinbergen's fundamental belief in the efficacy of Darwinian filters was brought to bear on his extensive knowledge of gull-nesting biology, the result was a specification of the mechanism that constituted the filter for eggshell removal.

The Tinbergen example illustrates the special role that a Darwinian filter explanation plays in guiding the research of a dedicated evolutionist. A filter explanation serves to focus the investigator's search for the causal mechanism that constitutes the filter. This heuristic value of a filter explanation depends on the degree to which making the explanation leads to a further specification of the way the processes of nature come to act as a filter. And the degree of specification of the filter depends, as we have seen, upon the degree of specification of the thing we are trying to explain. Perhaps Tinbergen's greatest talent as a scientist lay in his ability to ask questions at an appropriate level of generality. Had he asked only narrow questions, such as "Why does this species of

gull remove its eggshells?" or broader questions, such as "Why are gulls so successful?" he might never have been led to the crucial comparison with cliff nesting gulls which do not suffer from such severe egg predation and have not, as a consequence, been selected for eggshell removal.

For a Darwinian scientist speaking with other Darwinian scientists the primary value of filter explanations is a heuristic value. Since heuristic value is maximized by descriptions at a moderate level of generality, serious Darwinian scholars of animal behavior must focus their attention on what sorts of questions are likely to be the most productive. And since filter explanations are recursive and dependent for their quality on the quality of the question to which they are the answer, Darwinians cannot afford to ask questions at any level of generality and only worry about the generality of their answers. They must ask the right questions.

This principle may, upon sober consideration, cast doubt on some of the hottest research issues of the day. To ask questions like, "Why is behavior optimal?" or "Why is it altruistic?" may specify filters too broad to provide much guidance. It's hard to imagine scientists searching profitably for an optimality filter or an altruism filter. At the other extreme, asking questions like "Which variable is this species optimizing with its feeding behavior?" may lead to fragmented principleless accumulation of data. Creative use of Darwinian filter explanations requires asking questions that lead to the kind of comparative description that lay at the core of Tinbergen's most creative work and which, unfortunately, has largely gone out of style in recent years.

The ideal question consists of a search for an explanation of general principles that characterize the traits of organisms in relation to their circumstances. As a prelude to that search, we must of course define those principles. The candidate descriptive principle that we recommend most highly is the principle of adaptation, that which was closest, we feel, to Darwin's original intent. The best question for comparative psychologists to ask is why organisms are adapted to their environments. By "adapted" we do not mean of course, reproductively successful, because that would turn the explanation into the vague question cited above. We do mean by "adapted," more or less well designed for the circumstances of their existence. Consequently, asking the question entails the kind of exhaustive descriptive analysis of the concept of adaptation so often recommended (Sommerhoff, 1950; Thompson, 1986b, 1987; Williams, 1966; Curio, 1973) but rarely embarked on. Because of the recursive structure of Darwinian explanations, this descriptive analysis is crucial to the future of all Darwinian sciences—including comparative psychology—and it cannot be further delayed.

In considering the proposal that they take up the descriptive study of adaptation, psychologists should remember that behavioral adaptation occurs at two levels of analysis central to their field: the level of the species and the level of the individual. We can ask, for instance, why the behavior of species members is on the whole adapted to their ecological circumstances. This is the appropriate question for natural selection theory to answer. We can also ask, however, how individuals' behaviors come to be adapted to the flux of conditions in their moment-by-moment and day-to-day lives. This, of course, is a question of the motivational design of behavior, and is, we think, the appropriate question to be approached by a modern and ecologically sophisticated version of the other filter so central to comparative psychology: learning theory. Together, we think these two questions, and the relationship between them, deserve to be the proper domain of a newly constituted field of animal behavior, ethology, behavioral biology, or what-have-you (Thompson, 1986b, 1987). This new animal behavior field will be more theoretical than classical ethology but more descriptive than classical experimental animal psychology and contemporary sociobiology. And because it is attentive to the logical structure of its two central explanations, it will avoid the metatheoretical wrangling that has characterized the study of behavioral evolution in both its recent and more distant past.

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COMMENTARY

THE DIFFERENCE BETWEEN A CIRCLE AND A SPIRAL MAY BE SMALLER IN LEARNING THAN IN EVOLUTION

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It seems to me that Darwin's theory of natural selection *per se* explains one thing only, and does it neither circularly nor recursively: it explains how the structure of the environment can constrain inheritable characteristics of organisms so as to produce the otherwise inexplicable "fit" of organisms to environments (see Rozin & Schull, 1988). By providing this explanation, Darwin's theory enables us to generate *other* accounts, which explain particular organismic characteristics (*e.g.*, polar bear fur) via particular aspects of environmental structure (*e.g.*, arctic climate). These aspects of the environment are implicitly or explicitly posited to affect reproductive success, which, by virtue of Darwin's theory, could have caused the trait in question to have evolved. It is these "second-order" Darwinian accounts to which Lipton and Thompson's (1988) interesting analysis applies. So, for example, an account which says that fibers of polar bear fur conduct photic energy to the bear's skin has explanatory content only because Darwin's theory tells us how heritable, fitness-enhancing, characteristics will be treated by natural selection.

Now, when Lipton and Thompson (1988) suggest that their "comments about the logical vulnerability of Darwinian theory will have relevance to learning theory" (p. 2), it is presumably "instrumental learning theory" of the Thorndikean/Skinnerian sort to which they refer, for it is here that the analogy is clearest between environmental reinforcement of variant responses in ontogeny and environmental selection of variant genes (or traits). So, given Lipton and Thompson's analysis, can it now be said that instrumental learning theories, like Darwinian theories, are powerfully recursive? I'm not sure.

Instrumental learning theory has a vulnerability which goes beyond that imputed to Darwinian theory. Darwinian theorists, even if they acknowledge that not all traits are evolved *adaptations* (Gould & Vrba 1982), can presume that all species-typical characteristics have at least gone through the Darwinian filter which weeds out fatally maladaptive characteristics. Furthermore, Darwinian theorists can be confident that natural selection is relevant whenever species and organisms are reliably "improved" by interaction with their environments, since Darwin's theory remains the *only* explanation of how complex adaptations can evolve in an entropic universe. Even the acquisition of new adaptive behaviors is necessarily due to natural selection (Lorenz, 1965), since the ability of organisms to benefit from the vicissitudes of experience is itself an improbable characteristic of organisms which would be mysterious if not for Darwin's theory. These same abilities *also* require developmental explanation, of course, but that explanation *need not necessarily* involve reinforcement—there are other ways in which new adaptive behaviors can arise in ontogeny. (Pavlovian accounts of foraging behavior and food recognition provide a relatively well-studied example [Williams, 1980; Rashotte, O'Connell & Beidler, 1982; Rozin & Schull, in press;]).

This means that while the analogy between the theory of natural selection and Thorndike's theory of reinforcement is quite strong, the explanatory force of each is not the same. Darwin was able to argue that natural selection is a necessary consequence of certain *undeniable facts* about the biological world: that individual differences are inheritable, that some of them affect reproductive success, and that organisms produce an excess of offspring. Thorndike was only able to argue that instrumental learning *could explain* ontogenetic adaptation if we make certain *assumptions* about organisms: that behaviors vary within individuals, that this variation is due to stimulus-response connections, and that these connections can (somehow) be appropriately strengthened or weakened by the consequences of the behaviors they produce. Furthermore, we know that those assumptions can *not* be safely applied to all animals, nor to all behaviors, but we don't know, a priori where they do apply.

For example, suppose it were established that hungry animals who engage in a particular foraging behavior consume more food than animals who do not. If it could also be established that the behavior was heritable, it would be surprising if the behavior was *NOT* being favored by natural selection. In contrast, the analogous demonstration that the behavior was learnable-through-reinforcement, would leave wide open the question of whether it had in fact been learned, not to mention learned in the way instrumental learning theory implies. Animals do *NOT* always learn to do the things which maximize their rate of food intake (Kamil, Krebs, & Pulliam, 1987), and even if they do, the learning is not always of the instrumental sort. When the putative reinforcers in

question are conditioned, or otherwise are not obvious, it is even more difficult to establish the relevance of the account being offered. Indeed, in such circumstances, the only evidence for the existence of a reinforcer may be the occurrence of the behavior the reinforcer invoked is to explain.

In terms of Lipton and Thompson's analysis, these differences suggest that the explanatory content of instrumental accounts of adaptive behavior is greater than that of Darwinian theories, because instrumental learning accounts must assert the relevance of reinforcement theory itself, and not just the relevance of some particular reinforcers. By the same token, however, a larger burden of proof rests with the instrumental learning theorist, for the face validity of the assertions is necessarily less. I am willing to agree that instrumental learning theories, like Darwinian theories, are recursive and not circular. I think the current literature on learning mechanisms of optimal foraging demonstrates that they are heuristically powerful as well. But the situation confronting those who wish to develop and apply this kind of theory to learning is not the same as that confronting Darwinian theorists. Thus, while Lipton and Thompson may well have shown that Darwinian theorists theorize in spirals rather than circles, it is possible that until learning theorists can independently demonstrate that their favored explanations are not gratuitous redescriptions of the phenomena to be explained, the difference between a circle and a spiral will not be as great as we might hope.

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COMMENTARY

WHY BRING DR. PANGLOSS INTO COMPARATIVE PSYCHOLOGY?

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Lipton and Thompson (1988; henceforth L&T) have clearly been very much influenced by what they perceive to be the success of the adaptationist program in the study of evolution, and argue that it should play a major role in psychology as well. They are, however, aware that the program has been heavily criticized on grounds of circularity, and so they attempt to show that while adaptationist explanations may look circular, they are actually something different, which they call recursive. They then claim that Darwinian filter (i.e., adaptive) explanations are a special case of recursive explanations and therefore also not circular. In fact, there is nothing special about the so-called recursive explanations, and they therefore do nothing to improve the status of the kinds of filter explanations that are used in evolution theory.

The obvious way to define adaptation is in terms of natural selection: the better adapted organism is the one that is likely to leave more offspring. This is clear but circular, because it makes natural selection the survival of those that survive. Many authors consider this unsatisfactory, and some (e.g., Lewontin, 1978) have therefore proposed an alternative definition according to which an organism is said to be adapted if it has found an effective solution to some characteristic problem posed by the environment. This is less clear, but appears to avoid circularity. In fact, however, it does not, because there is really only one problem that the environment poses, that of surviving and leaving offspring.

Sometimes, to be sure, we may think we can identify a definite sub-problem. The approach may then have heuristic value, but nothing more than that, since it is only by knowing the solution that we can be at

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all sure what the sub-problem really was. For example, the basic assumption of optimal foraging theory is that organisms are trying to maximize their net energy intake. When Orians (cited by Lewontin, 1978) found that some birds did not behave as the theory predicted, he concluded not that they were poorly adapted, but that they were balancing the need for efficient foraging against the need to defend their nests. He may well have been right, but it is clear from his argument that the real problem was survival and reproduction, not energy intake. The birds that survive are those that survive, not those that find the most efficient foraging strategy. The same is ultimately true of all adaptationist accounts, however plausible they may appear.

L&T begin their proposed improvement on this situation by considering the question "Why are polar bears white?" They point out that the answer "Because they are white" is circular but that the answer "Because there is a force in the environment that makes them white" is not. Since the second answer, like the first, contains the explanandum in the explanans, L&T argue that it is a special kind of explanation which they call recursive.

Is there really anything special about the second answer? Surely not. After all, it could equally well have been "Because of a force in the environment." This tells us everything that the so-called recursive answer does, but does not contain the explanandum. The inclusion of the explanandum in the explanans is therefore unnecessary, and there is no need to consider its implications.

In general terms, consider the question "Why is E?" The answer "Because of E" is obviously circular. Suppose, however, that we have the perfectly ordinary, noncircular (and, let us suppose, correct) answer "Because of X." Then X is the cause of E. Hence if we answer "Why is E?" by "Because of X which is the cause of E" we have nothing more or less than "Because of X" and so there is nothing special about the longer answer except that part of it is redundant. It is this, and not "Because of the cause of E" that is the form of L&T's answer "Because there is a force in the environment that makes them white." "Because of the cause of E" translates into "Because of the cause of whiteness in bears," which, as L&T acknowledge, is circular unless we consider it as the negation of the hypothesis that the whiteness has no cause.

The answer "Because of X which is the cause of E" is different from "Because of X" only if we know in advance that X is the cause of E. In the case of L&T's polar bears, that would require that we could predict that the (arctic) environment necessarily made bears white even before we had ever seen a polar bear. But this is not so; after all, there are other large animals (humans, for example) who live in the arctic and are not white.

To use a real example, instead of a hypothetical one, to answer "Why do birds forage optimally?" by "Because of a force in the environment

that makes them forage optimally" and to claim that the last five words contribute anything to the explanation, we would have to know that there was an optimal foraging force in the environment, i.e., a force whose action is to make organisms forage optimally. But we know that there is not, or rather (and this is what matters) we know that those who use such arguments don't think there is. For from Orians' account cited in Lewontin (1978) it is clear that they believe only that there is a force in the environment that makes birds behave so as to maximize their chances of surviving and leaving offspring. Only after we discover that a certain species forage according to the predicted optimal pattern may we infer that there is a force in the environment that causes this species (but clearly not all species) to forage optimally. Optimal foraging theory therefore answers the question "Why do (some) birds forage optimally" by "Because of a force in the environment," and if we add "which makes them forage optimally" then, as explained above, we have contributed nothing to our understanding of the situation.

Where the theory can provide a useful heuristic is not in its answer to "Why do (some) birds forage optimally?" but in helping us to understand why certain birds forage in a certain way, which may be interesting but is not the same question.

When L&T come to discuss filter explanations, they change their position from what it was in the discussion of recursive explanations. They now write as though the nature of the filter were indeed known in advance. They answer "why are all the X's Y?" by "Because they have passed through a Y-filter," not "Because they have passed through a filter which made them Y." In the former case Y is a modifier of the word filter; we are told that the filter has the property that it makes things Y. In the latter case, we are told only that the effect was caused by a filter, which is new information, and that the result was that all the X's are Y, which we already knew. But it is the latter case that was discussed with regard to recursive explanations, and which corresponds to what those within the adaptationist programme actually assume.

Referring to Orians' example again, we cannot claim that organisms forage optimally because they have passed through an optimal foraging filter. The most we can say, if we employ this form of explanation, is that they have passed through a natural selection filter, which in some cases has picked out optimal foragers and in others has picked out less-than-optimal foragers whose behaviour conferred other advantages. This is just another way of saying what we said before, that ultimately adaptation is definable only in terms of survival and reproduction. L&T's analysis takes us no further ahead.

That the principle of natural selection is circular does not mean that it is without value. After all, mathematical theorems are tautologies too. It does, however, mean that the only part of the theory of evolution by natural selection that is not circular is its claim to be a sufficient account

of evolution (Maynard Smith, 1969) and it is largely on account of this that the theory is unfalsifiable (Saunders & Ho, 1982). The assumption that all traits of organisms owe their origin to the natural selection of small random variations is never questioned because the structure of the theory does not allow it to be. Instead, one takes it for granted and proceeds to decompose organisms more or less arbitrarily into traits, postulate some selective advantage of each of them (selective advantages are typically very difficult to measure, especially since in evolutionary studies one is so often speculating about the past) and claim thereby to have explained how each of these traits evolved.

This research strategy, sometimes called the "Panglossian paradigm," is inadequate even for the study of physiological evolution, but at least there it is generally possible to agree whether a character is heritable, even if there is room for dispute about how it evolved or even whether it evolved as an independent trait at all. (e.g., Gould & Lewontin (1979), especially their discussion of the human chin.) It is far less clear what is innate in human behaviour, so sociobiologists tend simply to fasten on a trait that "everyone knows" is innate, such as aggression, or male promiscuity, or incest avoidance, or whatever. They then look for a plausible selective advantage for the trait, and because their theory is unfalsifiable they eventually find one. This is taken to be both an account of how the trait evolved and—by implication—proof that it actually is a trait and that it is innate (Saunders, 1988). The adaptationist programme thus supplies pseudo-scientific backing for what are frequently only prejudices on the part of the writer, and we would expect that its application in psychology will lead to analogous errors.

To those outside the field, the neo-Darwinist theory of evolution may appear as a hugely successful theory which has accounted for almost all of evolution, leaving but a few details to be tidied up. In fact, the reverse is true: it may provide explanations for details such as the coloration of the peppered moth—though even that classical example is by no means as well established as is usually claimed (see Lambert, Millar & Hughes, 1986)—but it has very little to say about the major issues, apart from statements of faith that all of evolution is nothing but industrial melanism writ large. More and more workers within biology are abandoning the approach; instead of concentrating on natural selection they are seeking to account for evolution using the same sorts of explanation that are used in the rest of science, i.e., in terms of the processes that generate forms and variations at every level from the molecular to the sociocultural. (e.g., Ho & Saunders, 1984; Pollard, 1984; Ho & Fox, 1988.) There can be heuristic value in asking what function something serves, but we see nothing in the adaptationist program, either its

record in biology or the logical structure of its explanations, that should commend it to psychologists as a major component of their research activities.

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RESPONSE WHY DR. TINBERGEN IS MORE SOUND THAN DR. PANGLOSS

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We know that the editors have chosen their peer-commentators well because we find our position assaulted with equal skill and vigor from opposite directions. On the one hand, Saunders and Ho (1988) take us to task for having so much faith in the neo-Darwinian synthesis as to fall prey to Panglossian adaptionism. On the other hand, Schull (1988) takes us to task for having so little faith in the neo-Darwinian synthesis as to place it on a par with its poor cousin, reinforcement theory.

We suspect that the concept of natural design lies at the core of the difference between ourselves and our critics. Central to our argument is the idea that the behavior and morphology of organisms is characterized by two design properties, adaptation and purpose. Following Ryle (1949), Somerhoff (1950), Tolman (1951), and Hofstadter (1941), we think of these design properties as higher order characteristics of organism, similar to dispositional properties such as brittleness. These properties are not explanatory in any sense. To say that an animal's morphology is adapted or that its behavior is purposive is no more to explain it than saying that a lemon is yellow explains the lemon.

Both critics seem to doubt our assumption that adaptation or purposiveness can be recognized independently of the concepts that are deployed to explain them, natural selection and reinforcement. Saunders and Ho doubt that adaptation can be recognized except in reproductive success. Although he doesn't explicitly say so, Schull seems to doubt that we could ever make good on our commitment to identify the things toward which animals strive independent of their capacity to reinforce instrumental behaviors.

Identifying these properties in organisms in nature independent of their explainers is not easy but it is surely not impossible. The key is the comparative method. Just as it is possible to identify a property of adaptation by comparative analysis of species in relation to their environments, so it is possible to identify a property of purposiveness in the

behavior of individual animals by comparing the individual animal's behavior in relation to its circumstances. And just as you don't need to know how many eggs a woodpecker has to know that its beak is adapted to hammering wood, you don't have to know how many times a rat has been reinforced to know that its present behavior is directed toward discovering food. Like adaptation, purposiveness is a property observable in the behavior of animals.

Having begun with these general comments, let us proceed to consider some particular points.

(1) We are not—repeat *NOT*—apologists for Panglossian adaptionism. In its strongest form, we take the Panglossian position to be that Everything is Adapted and that All Adaptions are Selected. We disagree with both statements. We do, however, believe that some things are adapted and that some of these are selected. Adaptation is a property frequently observed in organisms and natural selection is often a reasonable explanation of that property. One of us (Thompson, 1981, 1987) has urged scientists to pay attention to two crucial problems of our day. When do organisms display the properties of adaptedness and when not? And when is natural selection an appropriate explanation for adaptedness and when not? These questions envisage all sorts of phenomena not envisaged by Panglossian adaptionism. They envisage adaptations not caused by natural selection and they envisage natural selection causing properties of organism other than adaptedness. So, unless Saunders and Ho take the position that adaptedness is a property rarely observed in organisms or that when observed, it is rarely attributable to natural selection, then they cannot pick a fight with us over Panglossian adaptionism.

Schull, on the other hand, is correct to pick a fight with us. He clearly believes that natural selection is the only reasonable explanation for adaptation and that adaptation is what natural selection must necessarily produce. This belief causes him to drive a wedge between what he says is the strong explanation of Darwinism and the weak explanation of reinforcement theory. But because we believe that natural selection is only one of a handful of factors that explain adaptations and because we believe that natural selection produces aberrations as well as adaptations, we don't see the difference that he sees between reinforcement theory and Darwinian natural selection theory.

In particular we don't see the difference in predictive power of the two theories. If we saw a distinct pattern of directedness in the behavior of an animal, and we saw that the performance of some behavior would transport the animal to the goal conditions designated by that pattern of directedness, and finally we saw that the animal was capable of performing and remembering that behavior, we would be surprised if that animal did not learn the behavior. Schull is quite correct to observe that animals don't learn all useful behaviors. But as Saunders and Ho would be quick

to point out, species don't produce all useful adaptations. And the reasons seem to be the same: the species cannot evolve what it cannot first produce by recombination or mutation and then subsequently retain through inheritance. Similarly, the individual cannot learn what it cannot first perform through innovation and then subsequently retain through memory. But given that the starting conditions of variation and retention are met, *both* natural selection and learning seem to guarantee systematic change as a matter of logical necessity. Both theories predict that the changes would adapt the organism to its circumstances [or bring it closer to its goals] and these predictions have empirical content and can be falsified in both cases.

But even if learning theory is less well-founded than natural selection, that would not show—as Schull seems to suppose—that the two theories don't have the same explanatory structure. Schull's supposition is a non sequitur. The explanatory structure of a theory is not determined by its evidentiary status. Whatever their foundation, both theories are recursive filter explanations.

(2) What was for us the main point of the target article seems to have been missed by both commentators. We set out to explain for ourselves why it was that the problem of circularity in evolutionary explanation refused to go away. The literature is littered with statements of this problem and with purported solutions of it. Yet it keeps coming back. If circularity is such an obvious flaw in the theory, why do brilliant people seem to still be prey to it? And if it's not a flaw, why do other brilliant people seem to bemoan it?

We think that the target article solves the problem of the recurring circularity problem. The solution we offer is that both schools of thought are correct. The people who say that the theory is not circular (or tautological) are correct because strictly speaking it is not. On the other hand, those who say that the theory lays terrible traps for the unwary are also correct. In other words, just because evolutionary explanations are not circular doesn't mean that they can't be empty and silly. We hope that the target article will stifle forever the useless discussion about whether they are circular or not and begin a more useful discussion about when they are useful and sound and when they are empty and silly. It was on this controversial point that we hoped our commentators would focus.

When is an evolutionary explanation empty and silly? It is empty and silly whenever those that use them abuse the special structure of such explanations. Darwinian explanations are recursive and as such, they have two parts: a frame which specifies what kind of a recursive explanation we are employing and the contents of the frame, which specifies which particular form of that kind of recursive explanation we are employing. For instance, when Tinbergen said that he thought that gulls removed eggshells from their nests because the surface nesting environment selected such behavior he was making two points: 1. The

gulls' behavior and morphology is the result of a filter; 2. The particular filter is an "eggshell removal" filter.

Now, the first statement is clearly not circular. No mention is made of the explanandum in the statement. Nor is it empty. To say that something has been filtered is, as our article points out in detail, to say quite a bit about it. That is why we feel we have laid out, hopefully forever, the question of the putative circularity of evolutionary explanations.

The second statement does contain the explanandum, but it is not the whole explanation and consequently the whole explanation is not circular. To underline this difference, we called the whole explanation recursive because, while it is not a restatement of the explanandum, it does refer back to it, and that 'back-reference' can be the source of difficulties.

Our goal was to begin a discussion about when such back references were troublesome and when they were benign. We thought Tinbergen's use of such statements was a good exemplar because he managed to do good science while using them and we wondered why he had been so fortunate. We reasoned that because the answer (an eggshell removal filter) to Tinbergen's question, "Why do gulls remove eggshells?" contained the question, there must have been something particularly fortunate about Tinbergen's understanding of his own question that kept him out of trouble. To put the matter briefly, if all evolutionary answers contain their questions and some evolutionary answers are better than others, then perhaps the quality of the explanation has something to do with the quality of the question embedded in it. We suspected that Tinbergen has been particularly happy in his choice of *questions*.

What was the outstanding characteristic of Tinbergen's questions? Tinbergen was first and foremost a comparative ethologist. Instead of asking the question, "Why is this animal this way in this place?" as a freestanding question, he always asked it in the context of a whole series of additional questions: "Why are those other animals those other ways in those other places?" In other words, Tinbergen's questions were more inclusive than they appeared to be. Although he appeared to be asking a question about the nesting habits of a particular gull under a particular set of circumstances, he actually was asking a somewhat broader question. He was asking, how does it come about that the eggshell disposition habits of gulls are *adapted*? In asking a question at this intermediate level of generality he was avoiding two faults of much contemporary adaptionist explanation. He was avoiding the fault of ad hoc examination of the traits of individual species. And he was also avoiding the fault of characterizing his problem in such broad terms. (e.g., optimality) as to prohibit any useful examination of it.

In this respect, Tinbergen was profoundly different from Pangloss. Pangloss' fault was that he had no concept of "the good." Consequently, what ever happened became the good, simply by virtue of its having

happened. If his theory was that God arranges that the good always happens, then he should be able to specify the good in advance, and that Pangloss could not do. Tinbergen had a leg up on Pangloss. Because of his grasp of the comparative method and his vast knowledge of natural history, he had independent knowledge of the good. Unlike Pangloss, Tinbergen approached his phenomena with systematic and falsifiable expectations.

If there is any lesson from all of this, it is that evolutionary explanation requires comparative description. Why? Because evolutionary explanations are recursive and therefore contain within them a description of the thing to be explained. As such, the quality of the explanation relies on the quality of the description. Vague descriptions lead to vague explanations, ad hoc descriptions lead to ad hoc explanations. Thus healthy evolutionary explanation relies on a base of well-articulated and general comparative description.

Despite Schull's doubts, we think that the same general rules of thumb can be applied to recursive reinforcement theory. Just as rigorous evolutionary explanation begins with careful comparative description, so rigorous explanation through reinforcement theories requires careful description of purposiveness in behavior. A well-described explanandum is the key to a useful recursive explanans.

(3) Biological and psychological points aside, our critics seem to have made several mistakes that are more purely philosophical. Two of these seem particularly interesting. The first is that there is nothing special about recursive explanations; the second is that a theory cannot explain its own evidence.

According to Saunders and Ho, recursive explanations are not circular, but they are not different from normal (i.e., nonrecursive) causal explanations. Their argument is that, in answer to the question "Why is E," the normal answer "Because of X" can trivially be converted to "Because of X which is the cause of E." The only peculiarity of recursive explanations is that they contain a redundant clause. We are pleased that Saunders and Ho clearly recognize that recursive explanations are not circular, one of the main points of our article, but they should have given more credit to the distinction between a recursive explanation and a normal one. In a recursive explanation, the cause is only specified by reference to its effect. This is not normally the case. If we explain the Chicago Fire by blaming Mrs. O'Leary's cow, we have a normal explanation, since the cause is specified without any reference to its effect. You don't need to know about the fire to know the cow. By contrast, if we explain the presence of a given behavior by saying that there is a filter that selected for that very behavior, we only get a grip on a cause by reference to its effect. The relevant filter is only specified by reference to the resulting behavior.

Recursive explanations cannot be automatically converted into normal ones. The reason is simple: we sometimes do not have an inde-

pendent characterization of the cause to replace the recursive answer. Saunders and Ho seem to deny this. They argue that it is trivial to convert the recursive "Polar bears are white because there is a force in the environment that makes them white" into the nonrecursive "Polar bears are white because of a force." This is a confusion. What is the answer they are proposing to the question of why polar bears are white? If it is simply that there exists an unspecified force in the environment, this is no explanation at all, because it neither specifies the cause nor tells us anything about the kind of cause it is. There are many forces in the environment, most of which have nothing to do with bears. What is more likely is that they intend "a force" to mean "a force that makes polar bears white." This is a cause, but it is obviously recursively specified. We have no objection to the shorthand "They are white because of a force," except that it may camouflage the recursive structure of the explanation and so mislead us into thinking that there is nothing special about recursive explanations. There really are three types of explanations: normal, circular and recursive. To determine which type you have, first look at the answer, then compare it to the question. If the answer specifies a cause without any reference, explicit or implicit, to the question, then the explanation is normal. If it fails to specify a cause at all, but only restates the question, it is circular. Finally, if the answer does specify a cause, but only in terms of the question, it is recursive.

The second important mistake concerns the relations between explanation and evidence. In analyzing the quality of explanations, it often helps to distinguish two questions: "Is there good reason to think that the explanation is true?" and "Would it be a good explanation if it were true?" The answers to these questions may diverge. In the case of Moliere's explanation that opium puts people to sleep because of its dormative powers, the answer to the first question is yes and to the second, no: the explanation is almost certainly true, but it is a terrible explanation. There are also cases where we have very little reason to believe the explanation, but where it would be a very good explanation if it were true.

To avoid unnecessary offense, examples of these are left as an exercise for the reader. Saunders and Ho, and Schull seem not to make this useful distinction between the evidence for an explanation and its explanatory power. This may have led them to suggest that an explanation cannot account for its own evidence. Thus Saunders and Ho argue that looking for a biological sub-problem "may then have heuristic value, but nothing more than that, since it is only by knowing the solution that we can be at all sure what the sub-problem really was." Similarly, Schull seems to claim that if the only evidence for a reinforcer is the behavior to be explained, then the reinforcer cannot be used to explain the behavior. The general view they seem to hold is that an explanation is no good if the phenomenon to be explained itself provides an essential part of the evidence that the explanation is true.

This view, that "self-evidencing" explanations are bad explanations, may appear plausible, since these explanations seem circular. The evidence is supposed to support the theory while the theory explains the evidence. Nevertheless, there are perfectly good self-evidencing explanations (Hempel, 1965, 372-73). I may explain the distinctive tracks in the snow before me by saying that a person on snowshoes has passed this way, even if my only reason for believing this are the very tracks I am explaining. An astronomer may explain the red-shift in a star by telling us the star's speed of recession, even if she depends on the red shift itself to determine the speed. And self-evidencing explanations are virtually unavoidable when the explanation appeals to unobservable entities, such as subatomic particles and their ilk. Here it seems that the only evidence we have for the theory is the evidence it explains. Indeed there is a popular theory of inductive inference according to which almost all explanations turn out to be self-evidencing. According to this account, known as *Inference to the Best Explanation*, we infer from our evidence, to what would be the best explanation for that evidence (Harman, 1965; Lipton, in press). Of course a particular self-evidencing explanation may be very poorly supported by the available evidence, but you cannot show this simply by pointing out that it depends on the evidence of the phenomenon it is supposed to explain. As the examples above show, the fact that an explanation is self-evidencing entails neither that it is insufficiently supported by the available evidence, nor that it lacks explanatory power.

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HABITUATION IN THE SEA ANEMONE, (*ANTHOPLEURA ELEGANTISSIMA*): SPATIAL DISCRIMINATION

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ABSTRACT: The method of habituation was used to demonstrate that sea anemones are capable of responding discriminatively to two places stimulated on the column. Thirty sea anemones (*Anthopleura elegantissima*) in six groups of five anemones each were given habituation training using a 0.2 s pulse of shock at twice the voltage needed to produce a perceptible contraction. Shock was delivered at electrodes implanted on the column midway between the oral and pedal disks. The stimulus was repeated at 60 s intervals until the anemone failed to respond on three trials in a succession of five. Habituation was first produced at an arbitrary point A, then at point B, which was horizontally 10°, 15°, 20°, 45°, 90° or 135° distant from A depending on the group. The mean ratio of trials to criterion, B/A, was determined for each group. A sequential multiple regression analysis on the power polynomial of degrees separation between points A and B indicates that a cubic function best fits this spectrum of points, going from retention of habituation (inhibition of responding) at point B when B is near A to facilitation of responding as the distance between A and B increases to 45° and again changing to inhibition at greater separations between A and B. These results suggest that anemones have the rudiments of a receptive field organization made up of nervous and neuroid elements which enables them to discriminate between spatially separated stimuli.

The possibility that coelenterates may be capable of a simple discrimination, i.e., "a differential response to two stimuli which differ qualitatively or quantitatively" (Warren, 1934) is suggested by similarities in functioning of coelenterate nerve nets and higher nervous systems. Bullock and Horridge (1965, p. 460) state that "The structural and functional elements of the nervous system of coelenterates are not fundamentally different from those in higher animals." The formation of the impulse group or burst by the sense cell-nerve net junction represents probably the first nervous integration in evolution. A neuroid and a nervous system provide the basis for conduction, transmission, and integration of information. Mackie (1970) associates neuroid conduc-

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tion, i.e. nonnervous epithelial conduction, with defensive and locomotor responses which are general in nature, whereas he suggests that more complex and local responses may be organized by the nervous system. The latter is a peripheral neural network with no centralization into ganglia and which includes a synaptic system (Westfall, 1973). Recent research indicates that information storage in nervous systems is not restricted to higher nervous systems nor to specific parts of the nervous system (Black et al., 1987).

One of the simplest behaviors that involves such information storage is habituation. This has been demonstrated in many invertebrates including sea anemones (Jennings, 1905). To date stimuli to which anemones have been experimentally habituated include various forms of chemical, physical and electrical energy (Haralson, Groff & Haralson, 1975; Logan, 1975). At present habituation is considered to be nonassociative learning. Petrinovich (1973) pointed out that habituation displays several of the characteristics of associative learning (i.e., classical conditioning and instrumental conditioning) such as retention, spontaneous recovery and stimulus generalization; therefore it may be viewed as a kind of learned behavior.

In the course of studying habituation as a form of learning investigators also have used it as a means of studying perceptual behavior in various species of nonverbal organisms. Demonstrations of various forms of perceptual discrimination have been described in human infants using a procedure in which habituation to one stimulus was followed by habituation to another stimulus (Bornstein, Kessen & Weiskopf, 1976; Cohen & Salapatek, 1975). A similar successive habituation procedure was used by Peeke and Veno (1973) to study discrimination of conspecifics in fish. Male stickleback fish were introduced as stimuli into the territories of resident stickleback males and habituation of aggressive responding (bites directed at the stimulus fish) by the resident male was demonstrated. The same or a different stimulus fish was then introduced either at the same or a different place in this territory. Amount of aggressive responding during rehabituation varied as a joint function of change in the eliciting stimulus and of change in the place where the stimulus was presented, although the former was more effective than the latter. Underlying the use of this method is the assumption that during the course of repeated stimulation, the organism learns something about the stimulus. When the stimulus is changed, the organism orients to the change. This can be regarded as a discriminative response.

Observations on habituation to tactile stimulation in anemones and frogs indicate in both cases that, although lateral inhibition may be involved in the discriminative process, facilitatory effects of such stimulation are involved as well. Kimble and Ray (1965) stimulated tactually an area of the skin of frogs with a number 10 Von Frey hair and elicited a

wiping reflex. They found that "reflex habituation" (decrease in number of responses over days) occurred rapidly if exactly the same place was stimulated, but that "reflex potentiation" (increase in number of responses over days) occurred if stimulation occurred randomly at different places within the area that elicited the response. In habituation studies using *Anthopleura elegantissima* as subjects, Logan (1975) stimulated the oral disk with a pulsating jet of water and, in some cases, observed "potentiation" of responding during rehabilitation rather than retention of habituation. She explained that this result occurred possibly because of uncontrolled movements of anemones between stimulations and therefore different places on the oral disk were stimulated because the water pic was in a fixed position. These results are similar to those of Kimble and Ray and may therefore indicate the existence of some sort of organization of conductive and integrative elements in anemones into tactile receptive fields similar to those found in vertebrates.

Frazer, Janes and Haralson (1975) also reported such an area of response facilitation (an increase in responding at B compared with A) in *A. elegantissima* when tactile stimulation (prodding the column just above the pedal disk) was applied at a point B 20°-90° horizontally removed on the column from a previously habituated point A.

We report here a study using the method of successive habituation to investigate the ability of the sea anemone, *A. elegantissima*, to discriminate between two different places stimulated on its column. Because the study by Frazer et al., (1975) indicated that an area of response inhibition (retention of habituation at the second point) was flanked horizontally by an area of facilitation, we designed the present experiment to determine the extent of the facilitated area by interpolating more points of stimulation at B in the inhibitory area adjacent to point A and by extrapolating a point beyond 90° at 135°. We also sought to gain precision by using implanted electrodes to deliver light shock instead of stimulating by hand with a prod as was the case in Frazer et al. (1975).

METHOD

Animals and Maintenance

Thirty sea anemones of the solitary form of *A. elegantissima*¹ gathered from intertidal zones near Portuguese Bend, California, were used in this experiment. The anemones measured 4-6 cm across the oral disk not including measurement

1. The taxonomic designation *Cribrina xanthogrammica* represents an early possible choice of name for *Anthopleura xanthogrammica*. The species used by Haralson, Groff and Haralson (1975) was *Anthopleura elegantissima* and represents the solitary form of that species (Francis, 1979; Haderlie, Hand, & Gladfelter, 1980).

of extended tentacles. Upon arrival at the laboratory and prior to experimentation they were placed on smooth, flat stones to which they tended to attach and were maintained in filtered sea water at 16° C for two to six weeks in a community tank measuring 91 cm long, 46 cm wide and 40 cm high. The water was obtained from Marineland of the Pacific. The anemones were fed a 1 cm² piece of shrimp every 12 days. A 12 hour light/dark sequence was used in the laboratory with the light condition extending from 0600 to 1800 h.

Apparatus

Electrodes: The implantation technique used here was described in a technical report by Grass Instruments (1975). Electrodes for implantation in the anemones were made of teflon-coated stainless steel wire (Medwire Corp. Part No. 316 SS 5T). Pieces of wire were cut at the length required to be connected to the shock apparatus and polygraph. One mm of teflon was stripped off at one end of the wire. This was then inserted approximately 2 mm into the hollow of a .20 gauge syringe needle and the remaining length of insulated wire was bent back against the needle. The needle was then inserted into the column of the anemone, and the end of the electrode wire was held down with a finger as the needle was removed. This left the exposed 1 mm of wire implanted in the subject in a hook-like fashion. In this position the exposed end of the electrode was presumably adjacent to epithelial cells. A third (stainless steel plate) electrode was placed on the long wall of the experimental chamber, described below, equidistant from the two implanted electrodes. This served as an indifferent electrode.

Experimental Chamber: The experimental chamber used in this experiment was made of plexiglass and measured 30 cm long, 15 cm wide, 15 cm high and contained seawater 10 cm deep.

Stimulation and Recording: The active electrodes were used for both stimulation and recording. A Model S4 GR Grass Stimulator was used to deliver shock to the implanted electrodes. Shock level was determined for each anemone by obtaining an absolute threshold using the ascending method of limits. Threshold was defined as the voltage that produced a perceptible contraction of the anemone as seen on the polygraph record. Shock voltage used during the experiment was twice the value of absolute threshold and was applied for 0.2 s as a single positive-going square wave pulse. At that voltage a response was produced in all subjects on at least the first experimental trial. Interstimulus Interval (ISI) was controlled by a Lehigh Valley Atcotrol Type 305 timer. A Beckman Type RS Dynagraph with a type 462 amplifier was used to record behavioral output.

Procedure

On the day of experimentation an anemone attached to a rock was removed from the community tank and was implanted with two electrodes on the column midway between the oral and pedal disks. The period of food deprivation at the time of experimentation ranged from three to six days. Each anemone was

assigned randomly to one of six groups which differed with respect to distance between electrodes. This distance for the six groups was measured horizontally in degrees of arc around the column. The first locus, point A, was selected arbitrarily and the second locus, point B, was 10°, 15°, 20°, 45°, 90° or 135° from point A depending on group. Each anemone, still attached to its rock, was then placed in the experimental chamber. The electrode wire jacks were plugged into sockets connected to wires leading to the Grass Stimulator and to the polygraph. The anemone was then allowed to habituate to the apparatus for a minimum of 1/2 hr or until it was fully expanded.

Threshold voltage was obtained and experimental shock voltage determined for each anemone. The anemone was again allowed to recover.

When the anemone had fully opened habituation trials were initiated at point A. Shock was delivered on an FT 60 s schedule. This was an adequate period of time for enough recovery to occur so that a response to the next stimulus could be recorded. The anemone was not necessarily fully open at the onset of each successive stimulus. Response occurrence was monitored on the polygraph. When a habituation criterion of failure to respond (i.e., no change on the polygraph record during 3 s following stimulus onset on three out of five trials) was reached, the point of stimulation was immediately changed to point B and the same treatment continued on the same schedule at the second point B to the same criterion. This procedure was repeated until there were five anemones in each of the six groups.

RESULTS

The anemone's response to electrical or mechanical stimulation is a rapid contraction of the oral disk accompanied by folding inward of the tentacles. There also may be a contraction of the column, and the anemone becomes vertically shorter. Complete contraction results in a short rounded shape as the sphincter muscle at the top of the column and below the oral disk contracts over the retracted tentacles. At times tentacles forming the central ring may come erect in what appears to represent investigative orienting behavior. A movement of any kind that was perceptible as an increase in voltage output on the polygraph record during a 3 s period following stimulus onset was recorded as a response. Therefore any of the movements described above which were recorded by the polygraph were scored as a response. Scores representing number of trials to criterion at Points A and B were determined for each anemone.

A ratio score of trials to criterion at point B divided by trials to criterion at point A (B/A) was then computed for each anemone and this comprised the raw score that was used in the statistical analysis.

A one-way analysis of variance for independent groups over the six groups defined by the degrees of stimulus separation did not yield a statistically significant result, $F(5, 24) = 2.08$, $p > .05$. However this analysis treats the six levels of the independent variable as if they are

nominal differences, not the quantitative differences (degrees of separation) which they are. A sequential multiple regression analysis was therefore used because it regards the degrees separation as a single quantitative variable and analyzes the correlation between degrees separation and the response ratio. Since the scatterplot reveals a nonlinear relationship a regression of the response ratio (the Y variable) on the power polynomial of degrees separation was accomplished with the sequential multiple regression analysis. The first order polynomial indicates no significant linear relationship, $F(1, 28) = 0.27, p > .05$; the second order polynomial indicates no significant quadratic aspect of the relationship, $F = 1.56(1, 27), p > .05$; the third order polynomial reveals a significant cubic aspect, $F = 7.58(1, 26), p < .05$ with a significant fit to the third order polynomial which combines linear, quadratic, and cubic components, $F = 3.26(3, 26), p < .05$.

Figure 1 shows the curve representing empirical group means and the theoretical curve for the cubic polynomial which best fits the data.

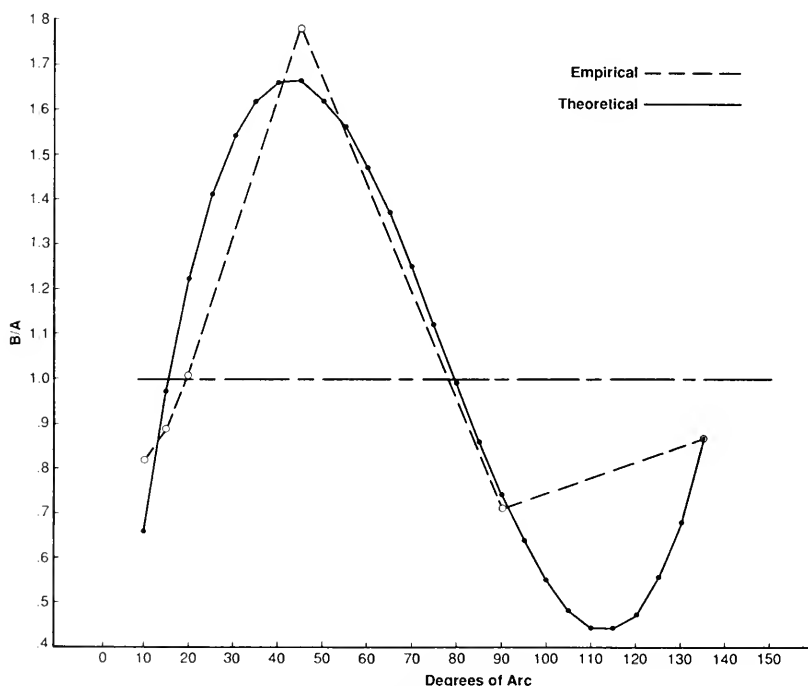


FIGURE 1

The empirical curve shows the mean ratio of number of trials to reach a criterion of habituation at B divided by trials to criterion at A as a function of number of degrees of arc separating A and B for each of six groups. The theoretical curve shows the cubic aspect of the data which was found to be the best fit to these data by using a sequential multiple regression analysis. Scores below the line at a ratio of 1 on the ordinate represent lower responding during habituation at B relative to A (retention of habituation, i.e., inhibition of responding); scores above 1 represent greater responding at B relative to A (i.e., facilitation of responding).

DISCUSSION

Since our procedure produced a quantitatively differential response at two spatially separated points of stimulation on the column, it appears that anemones are capable of discriminating between these points. Facilitation of the response occurs at point B if B lies between approximately 15° and 80° from A which is shown on the theoretical curve in Figure 1 as the degrees at which the curve crosses the horizontal line depicting a ratio of 1 or no difference in trials to criterion between A and B. This result is a replication and extension of Logan's (1975) observations on "potentiation" of responding during rehabilitation. The fact that differential responding is inhibited from 10° - 15° and again from 80° - 135° possibly implies that relatively little discrimination between A and B occurred when B was presented in either of these areas.

Such a pattern of tactile discrimination certainly is different from that found in vertebrates as described by Mountcastle (1961), Von Bekeasy (1967) and reviewed by Kandel (1981). It is, however, possible that our results represent the existence in coelenterates of the rudiments of a receptive field organization. If this is so, such an organization probably would involve conduction and integration in the nervous system as well as neuroid conduction as is suggested in Mackie (1970). Further research using other forms of stimulation as well as in different areas of the anemone's anatomy should reconcile these discrepancies.

Whatever the mechanisms underlying this behavior, it appears that we must entertain the possibility of advanced forms of neural conduction and integration in conjunction with neuroid conduction as the mechanisms in anemones which underlie the localized inhibition and facilitation of contraction to tactile stimulation as it was observed in this experiment.

A more thorough understanding of the relation of the behavior of *A. elegantissima* dealt with in the present study should result from the study of its interaction with the various animal species in its natural habitat. Most important for the purpose of understanding the adaptive significance of spatial discrimination would be to establish its function in the anemone's defending itself from important predators. For example the nudibranch, *Aeolidia papillosa*, attacks the column of *A. elegantissima* by taking large bites, then leaves to attack neighboring anemones, and returns to repeatedly attack those that have been previously bitten. The anemone characteristically responds to this predator by contracting, hardening its surface and, if it remains attached to the substrate, moving away from the nudibranch (Beeman & Williams, 1980; Haderlie et al., 1980; Waters, 1972). It would prove interesting to determine the relation, if any, of the spatial and temporal aspects of attack behavior by the nudibranch to the pattern of inhibition and facilitation of the ane-

mones's contraction response as it was observed in this experimental situation.

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ASSESSMENT OF VISUAL ACUITY, THE OBLIQUE EFFECT, AND THE LATERAL MIRROR- IMAGE CONFUSION EFFECT IN THE FERRET (*MUSTELA PUTORIUS FURO*)

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ABSTRACT: Visual acuity and the oblique and lateral mirror-image effects were assessed in adult fitch ferrets (*Mustela putorius furo*) tested on striped patterns in a two-choice apparatus for food. In Experiment 1, five ferrets were tested with the descending method of limits (obtained estimate, 17.67 min of visual arc) and the method of constant stimuli (estimate, 19.73 min of arc). Experiment 2 tested six ferrets on two target sets to assess the oblique and lateral mirror-image effects. Target Set 1 contained two pairs: horizontal/vertical and oblique (45°)/oblique(135°). Target Set 2 contained the same striped targets presented against gray targets. For each target condition, pairs were presented simultaneously and within the same session. Since acuity estimates were comparable for all orientations, there was no oblique effect. Rate of acquisition was not differential as a function of orientation for striped targets presented opposite gray targets, but was for simultaneously presented targets, i.e., oblique/oblique pairs were mastered more slowly. This was attributed to lateral mirror-image confusion, i.e., a mnemonic rather than sensory effect. The results are discussed in terms of species adaptation to habitat.

Comparisons of various species and their manner of function has been essential to the study of the vertebrate visual system (Polyak, 1957; Walls, 1967). While much comparative study has been devoted to primates (Allman, 1977; Van Essen, 1979; Weller & Kaas, 1982), the carnivores are represented in vision studies principally by the domestic cat, *Felis catus*, (Berkely, 1976; Boudreau & Tsuchitani, 1973; Spear, 1979; Van Essen, 1979; White & Ward, 1988). As useful as this well-studied carnivore has been to the understanding of visual function, it seems unlikely that one species could constitute a complete representation of carnivore visual adaptation.

The ferret (*Mustela putorius furo*) is a commercially available species approximately the size of a small domestic cat and is hardy, tractable, and docile (Hall, 1977; Willis & Barrow, 1971). This species was first

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domesticated from the European polecat, *Mustela putorius*, a burrowing predator of rodents and lagomorphs. By contrast, the cat is specialized for aboveground predation. The importance of vision to the cat is evident in its hunting style with prey slowly stalked until a quick rush is initiated, followed by a precise bite to the neck region that dislocates the vertebrae. This hunting style is strongly dependent on visual guidance. The ferret has smaller eyes than the cat and a hunting style evolved in colder climes where underground prey could be successfully pursued by scent-tracking in burrows, an activity that culminated in a coarse, crushing bite to the neck region of the prey similar to that killing style proposed for the earliest carnivores (Ewer, 1973). The retention of the primitive carnivore killing bite suggests that the ferret is a closer approximation to the ancestral carnivore than the cat.

Not only does the ferret offer to the study of comparative visual function a different carnivore adaptation pattern than the domestic cat and the possible phylogenetic advantage of greater similarity to carnivore ancestors, but also an advantage for the ontogenetic study of visual function since parturition occurs earlier in fetal development of the ferret than of the cat (Rowlands, 1967). The structure and function of the developing ferret visual system are thus more available for study. Although recent anatomical studies have taken advantage of these circumstances (Braekevelt, 1983; Greiner, 1981; Henderson, 1985; Linden, Guillery & Cucchiari, 1981), there has been little behavioral study of the visual capacities of the ferret (however, see Pollard, Beale, Lyons & Preston, 1967).

In the present study two experiments were conducted. In the first experiment the visual acuity of the ferret was assessed by both the descending method of limits and the method of constant stimuli to obtain a reliable estimate of this capacity that could be compared with that of the domestic cat. The second experiment employed two methods of stimulus presentation to determine whether or not the ferret is susceptible to the oblique effect. The oblique effect (also, orientation anisotropy) is the reduction in visual acuity for lines or gratings with diagonal as opposed to vertical or horizontal orientation. This effect is commonly found in species of primates (Bauer, Owens, Thomas, & Held, 1979; Bonds, Casagrande, Norton, & DeBruyn, 1985; Harwerth, Smith, & Okundaye, 1983; Mansfield & Ronner, 1978; Williams, Boothe, Kiorpes, & Teller, 1981), including humans (Gwiazda, Held, & Scheiman, 1984; Kitterle & Kaye, 1985; Taylor, 1963; Vandenbussche, Vogels, & Orban, 1986), but the question of the effect in cat remains unsettled (Bisti & Maffei, 1974; Parriss, 1964; Vandenbussche & Orban, 1983).

In these ferret studies two methods of stimulus presentation were used in order to assure that the oblique effect was measured and to assess the relationship between the oblique effect and the lateral mirror-image confusion effect. The lateral mirror-image confusion phenomenon

is manifest as the retardation of discrimination learning when one member of a figure or pattern pair is structurally identical to the other but is rotated 180° degrees about its median vertical axis. Thus, the oblique effect is properly measured as alteration of final level of performance, while the lateral mirror-image confusion effect is measured as retardation in the rate of learning. These two phenomena were confounded in the early oblique-effect literature (Appelle, 1972); therefore, the two methodologies of the second experiment were employed for the purpose of illustrating and clarifying this distinction.

EXPERIMENT 1

Method

Animals. Five adult fitch ferrets (*Mustela putorius furo*), two males and three females between 1 and 3 years of age, were trained and tested at 80% ad libitum body weight. Ad libitum body weights ranged from 1090 and 1170 g for males and from 620 to 774 g for females. Ferrets were maintained on a diet of Purina Cat Chow and raw liver. The animals were obtained from Marshall Research Animals, North Rose, New York.

Stimulus Materials and Apparatus. The targets used were pairs of alternating stripes with the width of each black or white stripe as follows: 2.5, 1.25, .63, .31, .16, .08, and .04 cm. The respective widths of black Chartpak graphic tape were aligned across white engineering tracing paper at intervals to produce alternating black and white stripes. These targets were sandwiched between sheets of 10 x 10 cm clear Plexiglas. When mounted in the apparatus the visible area of the targets was 8.97 x 8.97 cm.

The apparatus was a Yerkes two-choice box constructed from black Plexiglas and sprayed with flat black paint. The 16 x 46 cm enclosed startbox opened by means of a guillotine door into a 40 x 48 cm choice area. A central partition extended 30 cm from the stimulus display along the long axis of the rectangular apparatus and demarcated the choice point. The two alleys formed by this partition were 24 cm wide and terminated at the target display doors. An 8 cm Edwards bell made of cast metal with hammer action informed the subjects of incorrect choices. The bell was encased in a wooden box and mounted outside the apparatus in a central position behind the stimulus array. Food was dispensed following correct response by means of recessed food cups located behind the stimulus display doors. The targets were transilluminated by two 25 cm Sylvania fluorescent lights Model No. F15T12-CW mounted closely behind the target doors such that the near edge of the fluorescent tube was 10 cm from the rear of the target doors. Measurement of the transilluminated targets from a 30° angle at a distance of 45 cm by a Salford Electrical Instruments (S.E.I.) Exposure Photometer gave values closely distributed about 2.0 log ft-L. (342.64 cd/m²).

Procedure. The animals were deprived of both food and water except following their session in the test apparatus when free access to food and water

was given for 1 h. Performance reward was one part honey to two parts milk blended with 1 ml Polyvisol per 100ml fluid. Both food cups were baited with 1/2 ml fluid on every trial although the target door designated as incorrect on any trial was secured at the outer edge with a barlock so that food reward was never available on error trials. Subjects were trained and tested in sessions of 40 trials per day for all conditions and the running box was routinely wiped cleaned with Windex after each session.

Animals were retained in the startbox for 10 min before each daily session. At the beginning of each trial the ferret was released from the startbox and allowed to proceed to the choice point 30 cm from the target doors. If the subject entered the alley leading to horizontal stripes, the animal was permitted to proceed to the target door, push it with the nose, and take the liquid reward from the recessed foodwell. If the subject's nose entered the alley leading to the vertically striped target, the bell was activated and the subject was picked up and returned to the startbox by the experimenter to await the next trial. All subjects were trained to approach the horizontal stripes.

Two estimates were made of the resolution acuity threshold. First, a descending method of limits utilized the full range of target pairs. The criterion for target mastery was one day at 100% correct or two consecutive days at 90% correct. When a subject did not reach criterion but performed above chance on a given stripe width, the subject was tested for an additional 400 trials on the next finer stripe width. This phase of testing ended when the animal had attempted discrimination of a target pair for 400 consecutive trials with no improvement beyond a chance level of performance.

The second phase of the study employed the method of constant stimuli. In addition to the final target pair unmastered by each animal, the target pair immediately below (i.e., the next finer stripe width) and the two target pairs immediately above the failed target were presented ten times per session for five days. The four target pairs were presented within the same session with a different pseudorandom order for each session. Each of the four targets was presented a total of 50 times for a total of 200 trials.

Upon completion of testing, the refractive state of the eye was evaluated by two optometrists experienced in the use of this technique with nonhuman subjects. The visual acuity thresholds for both phases of Experiment 1 were estimated using the linear interpretation method of Guilford (1954).

RESULTS AND DISCUSSION

Visual acuity threshold estimates for individual subjects are presented in Table 1 as a function of the assessment method. The species estimate of ferret visual acuity was derived from the averaged thresholds of the five subjects and was 17.67 min of visual angle by the descending method of limits and 19.73 min of visual angle by the method of constant stimuli.

TABLE 1
Individual Estimates of Acuity as a Function of Test Method:
Experiment 1

<i>Subject</i>	<i>Retinal Angle (min)</i>	
	<i>Method of Limits</i>	<i>Method of Constant Stimuli</i>
Fm1	13.43	13.61
Fm2	13.34	15.95
Ff1	7.43	8.20
Ff2	27.84	30.44
Ff3	26.33	30.44
Means	17.67	19.73

It may be seen from inspection of Table 1 that acuity estimates for individual subjects were reliable across the two methods. There was some variability of acuity estimates among subjects that may reflect actual individual differences in visual acuity or, alternatively, the effect of nonvisual performance factors. Ferret Ff1 was, by all criteria, the best of the ferrets. She learned most quickly, responded most readily, and worked the choice point closely and carefully before each discrimination. Thus, it is likely that the threshold estimate for this ferret represents the best possible for a ferret with these stimuli and under these conditions of testing. Such individual differences in performance are often found in studies of animal visual acuity (see for example comments regarding subject 12 of Experiment 2 in Emerson, 1980).

The results of retinoscopy were that two of the subjects were found to be emmetropic (Ff1 and Fm2) and three were found to be slightly hypermetropic (Fm1, +1.25 each eye; Ff3, +1.50 each eye; Ff2, +0.75 each eye). However, since ferrets have small eyes, it is possible that the measurement of hypermetropia may have been due to the inherent error of retinoscopic technique with eyes of small diameter as reported by Glickstein and Millodot (1970). Nothing in the examination of the ferrets' eyes revealed a condition that might contribute to aberrant acuity estimates.

EXPERIMENT 2

Method

Animals. Six adult fitch ferrets, 3 males and 3 females aged 1-3 years, were tested to assess the oblique effect. Two of these ferrets (Ff3 and Fm2) had

been subjects in Experiment 1. The animals were trained and tested at 80% ad libitum body weight and maintained on the standard diet described above. Ad libitum body weights ranged from 1270 to 1620 g for males and from 655 to 930 g for females.

Stimulus material and apparatus. There were two sets of targets for Experiment 2. Target Set 1 was composed of two pair-sets: a set of horizontal versus vertical striped patterns and a set of oblique versus oblique striped patterns. Target Set 2 contained four pair-sets; each pair included one member of the pair that was a striped target, either vertical (90°), horizontal (180°), or oblique (45° or 135°), and a gray of matched luminous flux. The striped targets for all pair-sets had stripe widths of 1.25, 0.63, 0.31, and 0.16 cm respectively, and were constructed as those used in Experiment 1. Brightness values for the striped stimuli obtained with an S.E.I. Exposure Photometer ranged from 1.7 to 2.1 log ft-L (243.3 to 376.9 cd/m²). Translucent, homogenous gray Zip-a-tone art paper Nos. 2713, 2714, and 2715 with the respective measured brightness values of 2.0, 1.9, and 1.75 log ft-L (342.6, 311.8, and 260.4 cd/m²) was matched to each stripe width to compose the set of gray targets. The viewing area of all targets was a circle 5 cm in diameter located in the center of the target with the remainder of the target masked by black construction paper. Circular masks were used to avoid the enhanced distinctiveness of horizontal and vertical targets as compared to oblique targets when framed with square borders (Berkley, 1976).

PROCEDURE

The deprivation schedule, trials per daily session, reinforcement, and baiting procedures were identical to those of Experiment 1. Three ferrets were assigned to testing with Target Set 1 and the other three to Target Set 2. Within each target set two ferrets were assigned to one pair-member and one ferret to the other pair-member as the rewarded target.

Pretraining. Each subject received extensive pretraining on the 1.25 cm target pairs of the set to which it was assigned. Each pretraining target pair was presented singly within sessions until the subject responded correctly on 90% of 40 trials for two consecutive days. The order of pretraining within each of the target sets was: Target Set 1, first the horizontal versus vertical stripe targets, then the 45° oblique versus 135° oblique; Target Set 2, first the horizontal stripes versus gray, then vertical versus gray, next 45° oblique versus gray, and lastly, 135° oblique versus gray.

Testing. During testing all target pairs of each of the two target sets were presented concurrently within each daily session in a pseudorandomized order. Target Set 1 had two stimulus pairs that were presented 20 times each session for a total of 40 trials per session. Target Set 2 was composed of four stimulus pairs that were presented ten times each session for a total of 40 trials per session. Testing began with the 0.63 cm stripe targets for all target pairs. The descending method of limits was applied such that when one stripe width was mastered within a target set, discrimination testing of the next finer stripe width was begun in the same target set condition. The criterion for mastery was two consecutive days at 90% correct over all pairs within the assessment condition.

Testing ceased when performance was at the level of chance for ten consecutive test sessions.

A post-test was given to the three subjects assigned to Target Set 2. This post-test was designed to determine whether the ferrets were discriminating stripes from gray or possible variations in brightness that may have been discriminable to the ferrets. Each animal was given one session within which all orientations of the 0.63 cm stripes were paired with all three of the gray targets described above in three replications.

RESULTS AND DISCUSSION

Absolute thresholds for visual acuity were assessed as in Experiment 1 and are summarized in Table 2. The mean acuity estimates by test condition are somewhat higher for this group of subjects than for those of Experiment 1. When considered individually, the visual acuity estimates for these subjects are, in general, comparable to those of Experiment 1. The difference in the mean estimates between the two experiments seems largely due to the very low acuity threshold of one subject in Experiment 1, subject Ff1. In particular, comparison of visual acuity thresholds for the two ferrets that were subjects in both experiments indicates good correspondence between test methods: Ferret Fm2 had mean overall acuity estimates of 14.65 min of visual angle for Experiment 1 and 14.7 min for Experiment 2; Ferret Ff3 had estimates of 28.39 min for Experiment 1 and 34.82 min for Experiment 2.

TABLE 2
Individual Estimates of Acuity as a Function of Test Condition:
Experiment 2

<i>Target Set 1</i>			<i>Target Set 2</i>		
<u>Animal</u>	<i>Orientation</i>		<i>Orientation</i>		<u>Animal</u>
	<i>OB/OB</i>	<i>H/V</i>	<i>OB/G</i>	<i>HV/G</i>	
Ff4	29.73	32.20	34.63	35.0	Ff3
Fm2	14.73	14.67	19.84	22.87	Ff5
Fm4	31.06	34.84	14.66	14.53	Fm3
Means	25.17	27.24	23.04	24.13	Means

Note: Acuity threshold estimates are expressed as retinal angle in minutes of arc. OB/OB = oblique versus oblique targets; H/V = horizontal versus vertical targets; OB/G = oblique versus gray targets; HV/G = horizontal and vertical targets versus gray targets.

A determination of the presence of the oblique effect in the ferret required that measured acuity thresholds for the discrimination of oblique stripes be consistently higher than those obtained from the discrimination of horizontal and vertical stripes regardless of target presentation procedure. This difference in acuity threshold as a function of stripe orientation was not observed as illustrated by Table 2.

In the Target Set 2 presentation condition wherein each stripe orientation was discriminated from a gray target further evidence is found of the essential equivalence of stripe orientations in the assessment of visual acuity thresholds for the ferret. Using the threshold estimates shown in Table 3, a Friedman One-way ANDVA found no significant difference between the acuity estimates obtained from the two orientations of oblique targets and those obtained from horizontal and vertical targets.

There was, however, differential performance as a function of stripe orientation with Target Set 1 as shown in Figure 1 and thus evidence of lateral mirror-image confusion. Although the final level of performance as assessed by acuity thresholds did not differ by target presentation condition, the amount of training required to master oblique stripes discriminations was much greater than that required for the discrimination of horizontal versus vertical pairs. This was only true for the Target Set 1 presentation condition wherein striped targets were presented simultaneously within a trial and did not occur with Target Set 2 where striped targets were only judged against a gray target. Although mastery

TABLE 3
Individual Acuity Estimates as a Function of Stripe Orientation for Target Set 2

<i>Subject</i>	<i>Orientation</i>			
	<i>H/G</i>	<i>V/G</i>	<i>OL/G</i>	<i>OR/G</i>
Ff3	34.44	34.81	34.82	35.18
Ff5	21.29	18.48	26.76	18.97
Fm3	14.53	17.78	14.61	14.44
Means	23.42	23.69	25.40	22.86

Note: Acuity threshold estimates are expressed as retinal angle in minutes of arc. H/G = horizontal stripe versus gray; V/G = vertical stripe versus gray; OL/G = oblique slanted to left (135°) versus gray; OR/G = oblique slanted to right (45°) versus gray.

of the Target Set 2 problem required extended training, this was not differential by stripe orientation. The long period of training required for Target Set 2 may have been related to the fact that this set contained

four pairs of targets presented within one session as compared to the two pairs of Target Set 1.

Figure 1 illustrates the effect of lateral mirror-image confusion on the first test condition, i.e., the concurrent presentation of 0.63 cm striped targets. Thus while no oblique effect was measured for the ferret, the conditions for judgement of a lateral mirror-image confusion effect were met with Target Set 1.

When patterns of oblique stripes are presented simultaneously for discrimination, the greater difficulty in achieving these as compared to the discrimination of horizontal from vertical striped patterns is due to difficulty in remembering which of the two oblique orientations is the rewarded one (Essock, 1980; Fisher, 1982). Encoding of rewarded orientation was not required with Target Set 2 since all striped patterns were presented serially and discriminated from a gray target. Thus, it is concluded that serial presentation of striped targets is the best method to assess oblique orientation anisotropy.

It is also suggested that use of rate of learning rather than final level of performance to assess a basic sensory/perceptual capacity should be

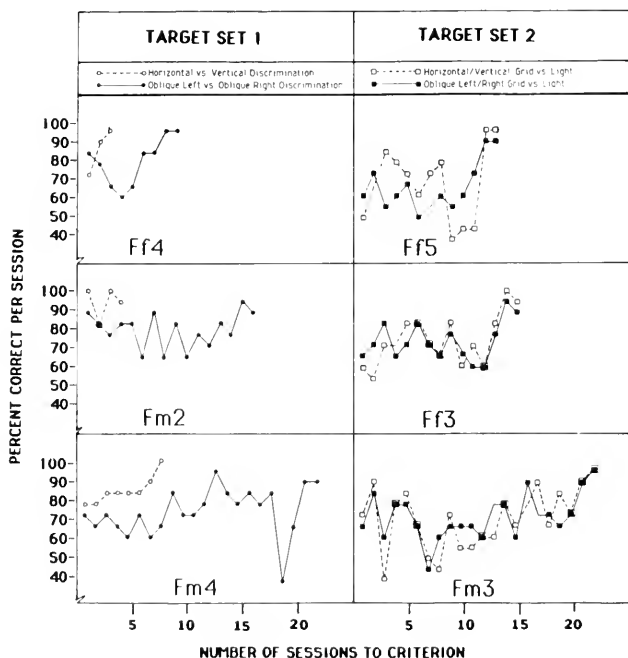


FIGURE 1

Performance of six ferrets tested in Experiment 2 to criterion on the discrimination of 0.63 cm separation striped targets presented either simultaneously (Target Set 1) or serially (Target Set 2).

avoided. Even with serial presentation of oblique stimuli, initial acquisition performance of animal subjects is influenced by so many variables not necessarily related to sensory/perceptual capacities as to make comparison of learning rates undesirable, especially with a limited number of subjects per condition. In a study of the oblique effect in the golden hamster (*Mesocricetus auratus*), Emerson (1980) presented gratings of various orientations to be discriminated against gray targets and found no evidence of an oblique effect in terms of elevated thresholds for oblique gratings but did find a slower rate of learning in the initial acquisition of the discrimination of gray targets from oblique as compared to horizontal and vertical gratings. However, as reported these learning rate differences apparently only occurred for the initial acquisition of the discrimination and were observed in a between subject design with only three subjects per group.

The design of this ferret study was somewhat different in that subjects were initially trained on each stimulus pair presented individually within sessions before being tested on assigned target sets of finer stripes presented concurrently within sessions. The pre-training was necessary because four subjects were naive to the apparatus and stimuli while two were carried over from Experiment 1 in order that threshold estimates might be compared for some subjects between experiments. It also seemed likely that initial learning with concurrently presented stimulus pairs might present an extraordinary level of difficulty for ferrets. Given a number of subjects that did not permit complete counterbalancing for order of presentation in pre-training, the effect of orientation of stripes on the initial acquisition was not assessed. Rather the dramatic differences in performance were found in the first test condition when pairs of stimuli mastered individually with 1.25 cm separation gratings were presented concurrently within sessions with finer gratings. In this within subject comparison, slower acquisition was observed for oblique targets presented simultaneously but not for oblique targets discriminated from gray targets. In the latter condition, ferrets had only to remember one cue, either always go to the gray target or always go to a striped target; in the simultaneous presentation condition, it was necessary to remember to approach the horizontal or vertical for one target pair and the oblique (45°) or oblique (135°) for the other. The greater difficulty experienced by ferrets for the simultaneously presented oblique/oblique pairs as compared to horizontal/vertical pairs points rather clearly to the mnemonic difficulty associated with lateral mirror-image confusion.

In the post-test of the Target Set 2 subjects, the animals' successful discrimination was maintained when gray targets of various brightness were presented against all of the 0.63 cm striped targets. The mean percent correct responses by subject were Ff3, 94.9%; Fm3, 92.3%; and Ff5, 84.6%.

GENERAL DISCUSSION

The resolving power of the ferret visual system is less than that of the domestic cat as would be expected from the relative importance of vision given the habitats and behavioral adaptations of the two species. As compared to the group estimate of ferret visual acuity threshold as 17.67 min of visual angle by the descending method of limits, cat acuity thresholds have been estimated at 5.5 min of visual angle (Bisti & Maffei, 1974; Blake, Cool, & Crawford, 1974; Campbell, Maffei, & Piccolino, 1973; Smith, 1936). Since the ferret with the best performance in this study was only able to achieve a threshold estimate of 7.43 minutes, it seems certain that the ferret has poor visual acuity as compared with the domestic cat.

The retinas of ferret and cat have an area centralis (Henderson, 1985; Prince, Diesem, Eglitis, & Ruskell, 1960) and contain both rods and cones (Braekevelt, 1983; Walls, 1967; Weidman & Greiner, 1984). The greater resolving capacity of cat vision as compared to that of the ferret may be related to the relative differences in the size and density of the retinal ganglion cells rather than differences in the receptor mosaic (Berkley, 1976). In ferrets, the cell bodies of ganglion cells in the area centralis are not consistently smaller than those in the periphery of the retina (Henderson, 1985); whereas in cats the cell bodies of ganglion cells in the area centralis are significantly smaller than those of the periphery (Boycott & Wassle, 1974). Further, the density of ganglion cells in the cat area centralis (Hughes, 1975), is twice that of the ferret (Henderson, 1985). Thus, differences in the structure of the receptor organ are congruent with the measured differences in behavioral capacity.

Ferrets exhibit lateral mirror-image confusion, as do some other mammalian species (Corballis & Beale, 1976; Riopelle, Rahm, Itiogawa, & Daper, 1964; Sanford & Ward, 1986), but fail to exhibit the oblique effect. It seems likely that the oblique effect is not prevalent among mammalian species and that at least some reports of the oblique effect may have confused it with lateral mirror-image effects. For example, almost all of the animal behavior studies cited by Appelle (1972) in a review of oblique effects were erroneously classified. In each of the studies cited, opposing diagonals, either rectangles or stripes, were the targets simultaneously presented for discrimination and rate of learning was the dependent measure employed. As demonstrated by the results of the present study, the use of these procedures results in the confounding of the oblique effect with the lateral mirror-image confusion effect. The term oblique effect as used by Appelle (1972) refers to at least two different phenomena. In current literature the term is used more or less interchangeably with the more precise term oblique orientation anisotropy. Since there appear to be at least two "oblique effects" (Essock, 1980), perhaps in the interest of clarity the use of the term oblique effect should be discon-

tinued and the term lateral mirror-image confusion used to refer to rate of learning effects and the term oblique orientation anisotropy employed when acuity threshold shifts are measured (White, Ward, & Bartley, 1988).

It may be that oblique orientation anisotropy is, in fact, characteristic of primates, if not unique to this mammalian order. Certainly, the question of orientation anisotropy in cats has received some study and the weight of evidence seems to support the view that the cat, like the ferret, is not much susceptible to this effect (Berkley, 1976) while primates typically display it. This difference between primate and carnivore may be a consequence of the effect of the more vertical neuraxis associated with arboreal habitat and/or bipedalism on visual function. It is possible that the elevated acuity thresholds of primates for oblique stripes represent not so much a deficit in capacity for discrimination of obliques as a relatively enhanced capacity for the perception of vertically and horizontally oriented lines and surfaces, a capacity that has been demonstrated to be preferentially associated with central visual fields.

It may be that oblique orientation anisotropy is, in fact, characteristic of primates, if not unique to this mammalian order. Certainly, the question of orientation anisotropy in the cat has received some study and the weight of evidence seems to support the view that the cat, like the ferret, is not much susceptible to this effect (Berkley, 1976) while primates typically display it. This difference between primate and carnivore (Simeonova & Vassilev, 1985; Vandenbussche, Vogels, & Orban, 1986) may have adaptive value for primate species. From this it might be predicted that not only cat and ferret but most quadrupedal mammals, when evaluated with proper procedures, would be found to have visual acuity thresholds that are independent of target orientation or perhaps favor other ecologically appropriate orientations. For example, the orientation anisotropy of the Mongolian gerbil, *Meriones unguiculatus*, favors the horizontal meridian (Baker & Emerson, 1983) as might be expected for a species that inhabits a desert or steppe-like environment with extensive level horizon. By contrast, human primates with upright stance as well as nonhuman primates in complex arboreal environments might well benefit from a visual system finely tuned to vertical and horizontal planes.

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